

Salp distribution and size composition in the Atlantic sector of the Southern Ocean

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Abstract

Salp abundance and length frequency were measured during the large-scale CCAMLR 2000 Survey conducted in the Atlantic Sector of the Southern Ocean in the 1999/2000 season. Results from regional surveys around Elephant Island in 1994/95 and 1996/97 seasons also were examined. During the CCAMLR 2000 Survey, salp abundance was higher in the Antarctic Peninsula and South Sandwich Island areas than in the central Scotia Sea. The probable reason for this pattern is a negative relationship with phytoplankton abundance; the central Scotia Sea having greater phytoplankton concentrations than required for optimal salp filter-feeding performance. Cluster analysis of salp size composition resulted in three cluster groups for each of the three surveys. Clusters comprising large salps occurred in warmer waters in all three surveys. The size composition of the salp populations suggests that the timing of intense asexual reproductive budding was earlier in warmer waters. As surface water temperatures generally decrease from north to south, and increase from spring to summer, the general spatio-temporal pattern of asexual reproduction by budding is likely to proceed from north to south as the summer season progresses.

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1. Introduction

The pelagic tunicate *S. thompsoni* occurs in dense swarms in Antarctic waters (e.g., Loeb et al.,

1997; Nishikawa et al., 1995) and has an important role in the Antarctic ecosystem. Owing to a high filtering rate, salps are serious competitors for the other herbivorous plankton species, such as Antarctic krill (Loeb et al., 1997; Perissinotto and Pakhomov, 1998; Siegel and Loeb, 1995). From a geochemical perspective, salps form an important component of the biological pump transferring carbon from surface waters to deeper

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layers (Perissinotto and Pakhomov, 1998). Salps are also consumed by a range of predators, mainly fish and birds, and are thought to have a more important role in the food chain than previously thought (e.g., Pakhomov et al., 2002). These studies indicate the need to establish the spatio-temporal distribution and abundance of salps. Salps reproduce rapidly under favorable food conditions (Alldredge and Madin, 1982) and exhibit patchy distributions. Does this mean that salp blooms are randomly distributed? Or do they exhibit trends in time and space? Such questions require a synoptic survey of salp demography together with other biological and environmental observations.

In the austral summer of 2000, the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) sponsored a survey—the CCAMLR 2000 Survey—in an area close to the Antarctic Peninsula. This paper reports on the spatio-temporal patterns of salp blooms in the Scotia Sea based on abundance and size composition data for *S. thompsoni* obtained during the

CCAMLR 2000 Survey (Trathan et al., 2001) and on data from smaller-scale observations around Elephant Island from two earlier seasons (Kattner, 1998; Kattner and Fütterer, 1995).

2. Materials and methods

The CCAMLR 2000 Survey took place during January and February 2000. Four vessels participated in the survey: the R.V. *Kaiyo Maru* (Japan), the R.V. *Atlantida* (Russia), the R.R.S. *James Clark Ross* (UK), and the R.V. *Yuzhmorgeologiya* (USA). Net sampling took place at the stations shown in Fig. 1 using an RMT1+8 (Rectangular Midwater Trawl; Baker et al., 1973). This was the standard sampling gear used on all four vessels (Siegel et al., 2004). This paper focuses on salps; further details concerning krill sampling are provided by Siegel et al. (2004) and RMT1 sample analyses by Ward et al. (2004). At each station, a quantitative standard double oblique tow was conducted from the sea surface to 200 m (or to

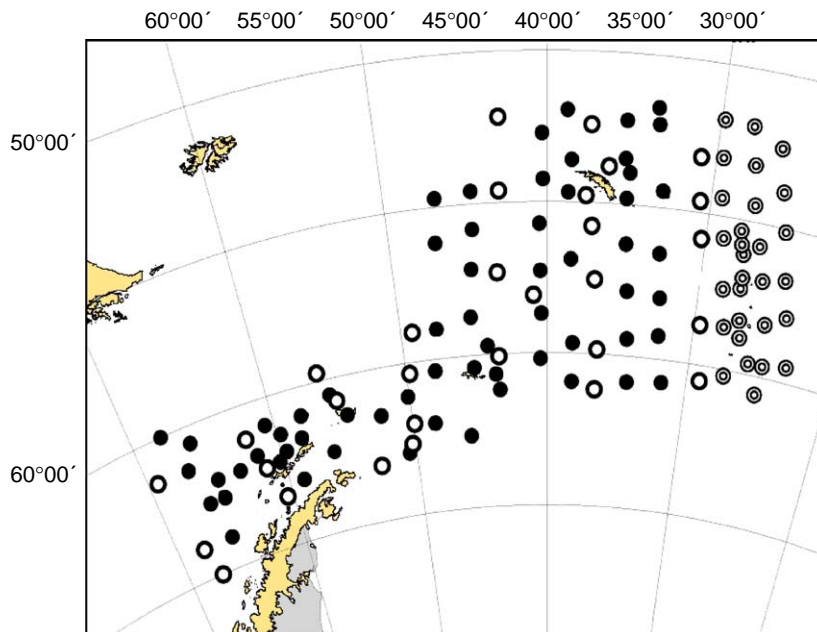


Fig. 1. RMT stations during the CCAMLR 2000 Survey. ●: Abundance and length measured for aggregate and solitary forms. ○: Total abundance measurements performed but length measurements only performed for aggregate forms. ⊙: Total abundance and length measurements.

within 10 m of the bottom at stations shallower than 200 m). The mesh size of the net was 4.5 mm, and the filtered volume during the tow was calculated by multiplying the mouth opening area (8 m²) by the distance of the tow determined using a flow meter.

Samples ranged in weight from a few grams to several kilograms. The total volume of the net catch was measured in terms of the total drained sample volume. For catches with a total volume of less than 1 l, the salps were counted immediately after the net haul.

For samples greater than 1 l, a random 1-l subsample was taken. *S. thompsoni* and *Ihleia racovitzai* were identified according to Foxton (1966, 1971). Few *I. racovitzai* were found in the study area (small numbers were observed at two stations only) and so *I. racovitzai* was not considered further. Onboard the *Kaiyo Maru* and *Yuzhmorgeologiya*, the aggregate and solitary forms of the salps were identified and measured separately. Onboard the *Atlantida*, the two forms were not distinguished. Onboard the *James Clark Ross*, the two forms were distinguished but length measurements were performed on the aggregate form only. This variation is shown in Fig. 1. Whenever possible, a minimum of 100 specimens per sample were measured. Internal body length (Foxton, 1966) was measured to an accuracy of 1 mm.

Surface chlorophyll (Chl-*a*) concentration was determined by filtering water samples through Whatman GF/F glass fiber filters or through membrane filters of 0.45 µm pore size (see Holm-Hansen et al., 2004).

Surveys in the Elephant Island area were undertaken by FS *Polarstern* (Germany) in the austral summers of 1994/95 and 1996/97 as part of the ANTARKTIS XII and XIV expeditions (Kattner, 1998; Kattner and Fütterer, 1995). Sampling protocols were basically the same as during the CCAMLR 2000 Survey, i.e. double oblique tows using an RMT-8 net to 200 m. Aggregate and solitary forms were identified, but internal body lengths were measured for the aggregate forms only.

Cluster analysis was used to compare between-station similarities in salp size composition. The

hierarchical fusion of clusters was performed using Ward's method to link homogeneous clusters, and the Euclidean distance coefficient was used for the similarity index. Only stations with at least 20 measured specimens were used in the cluster analysis.

Each length–frequency distribution was weighted by the size of the catch and the filtered water volume before the data were combined to provide composite length–frequency distributions. The Kolmogorov–Smirnov non-parametric test was used to test for differences in seawater temperature distribution (for 0–200 m) among the different salp size clusters.

3. Results

3.1. January/February 2000—the CCAMLR 2000 survey

3.1.1. Abundance distribution

S. thompsoni densities (aggregate plus solitary forms) are shown in Fig. 2. Although salps were found throughout the survey area, abundance in the central Scotia Sea was relatively low. At stations where the two sexual forms (aggregate/solitary) were identified, aggregates dominated in number (Table 1). The greatest densities occurred around the South Shetland Islands, the South Orkney Islands, and to the east of the South Sandwich Islands. Average density within the survey area was 83.7 ind/1000 m³. The highest density (1806.0 ind/1000 m³) was recorded to the northwest of the South Orkney Islands (58°53'S, 49°08'W; station JC26(2)).

The density distribution for the solitary forms is shown in Fig. 3A. Although the pattern of density distribution was similar to that for the aggregate and solitary forms combined (Fig. 2), abundance was considerably lower with a maximum of 3.7 ind/1000 m³ and a mean of 0.31 ind/1000 m³ for the Scotia Sea, and 6.0 and 0.73 ind/1000 m³, respectively, around the Antarctic Peninsula (Table 1). Relatively few solitary forms were found around the South Orkney Islands.

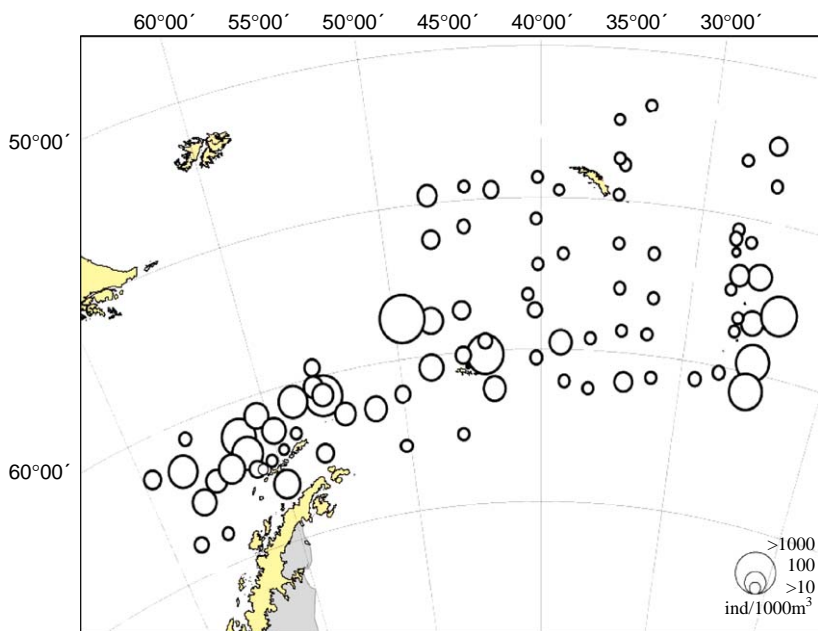


Fig. 2. Density distribution of aggregate plus solitary forms combined (ind/1000 m³).

Table 1
Salp abundance (ind/1000 m³) within the general Scotia Sea area during January/February 2000, and in the Elephant Island area during November/December 1994 and December 1996

	Solitary forms				Solitary + aggregate forms			
	<i>n</i>	Max	Mean	S.E.	<i>n</i>	Max	Mean	S.E.
Jan/Feb 2000								
Survey area	n.a.	n.a.	n.a.	n.a.	120	1806.0	83.7	20.7
SSI	n.a.	n.a.	n.a.	n.a.	31	712.4	74.2	32.9
SS	40	3.7	0.31	0.11	57	1806.0	61.1	34.0
AP	22	6.0	0.73	0.35	32	860.4	133.0	36.2
Nov/Dec 1994								
EI	n.a.	n.a.	n.a.	n.a.	77	43.2	3.8	1.0
Dec 1996								
EI	n.a.	n.a.	n.a.	n.a.	92	1041.4	110.7	16.6

n: number of stations; n.a.: not applicable; SSI: South Sandwich Island area (east of 30°W); SS: Scotia Sea area (50°–30°W); AP: Antarctic Peninsula area (west of 50°W); EI: Elephant Island area.

3.1.2. Length–frequency distribution

3.1.2.1. Aggregate form. For stations where the two forms were not separated, individuals >80 mm were removed from the length–frequency distributions, since these were obviously outside the size range of aggregate forms (Foxton, 1966). It was still possible that some solitary forms were

included in length classes <80 mm. However, since numbers of the solitary form are generally very low compared to the aggregate form (Table 1), the effect of including small solitary forms in the length–frequency distributions is probably negligible. To test this assumption, sub-samples from these stations were examined after the cruise.

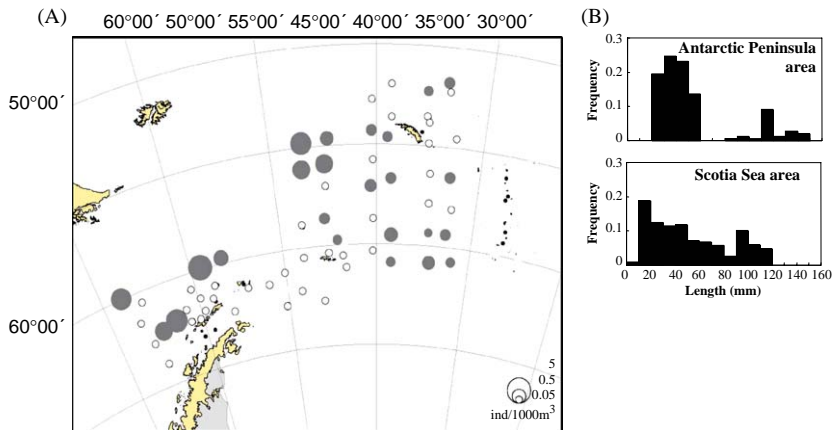


Fig. 3. (A) Density distribution of solitary forms only (ind/1000 m³). Open circles denote stations with zero catch. (B) Size distributions for the Antarctic Peninsula area and the Scotia Sea.

Analyses confirmed that the numbers of solitary forms inadvertently included were indeed negligible.

At a similarity level of 0.8, the length–frequency distributions clustered into three groups of stations (Fig. 4A). Fig. 5B shows the length distribution of each cluster. Cluster 00A mainly comprised 14–62 mm salps and had a modal length of 34 mm; Cluster 00B comprised salps of 8–44 mm and had a modal length of 26 mm; Cluster 00C comprised 4–40 mm salps and had a modal length of 12 mm.

The spatial distributions of clusters 00A, 00B, and 00C are shown in Fig. 5A. Cluster 00A, the largest size group, mainly occurred in deep water offshore of the South Shetland Islands, to the northwest of the South Orkney Islands, and in the Bransfield Strait. Cluster 00A also occurred at the northern edge of the survey area in the central Scotia Sea, but density was low. Cluster 00B, the medium-size cluster, occurred along the northwest side of the South Shetland Islands, but more inshore than Cluster 00A. Cluster 00B extended to the east beyond the South Orkney Islands and also was observed to the north of the South Sandwich Islands. Cluster 00C, which represented the smallest salps, was most abundant to the east of the South Sandwich Islands. Low numbers of these small salps also occurred along the southern edge of the survey area in the eastern Scotia Sea, and in the central Scotia Sea. Many of these

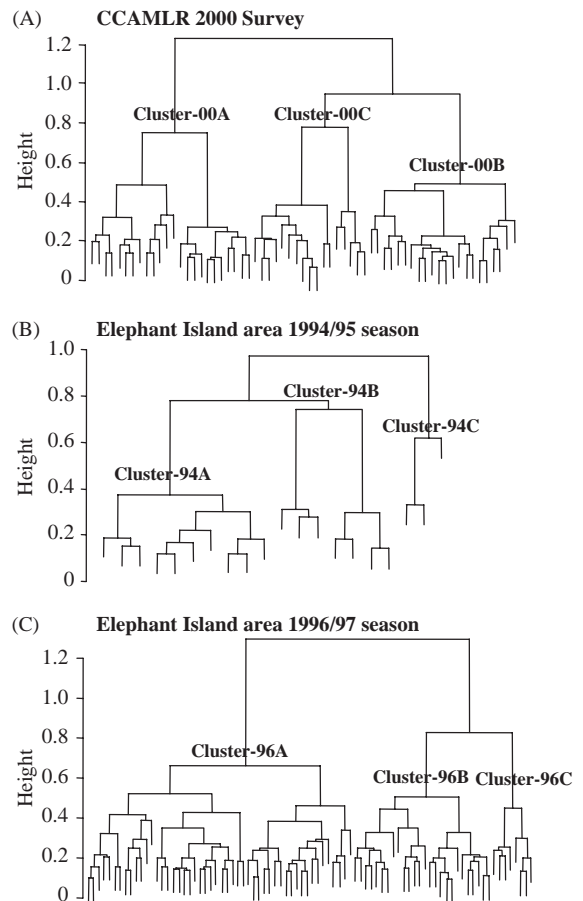


Fig. 4. Dendrogram resulting from cluster analysis of salp size groups.

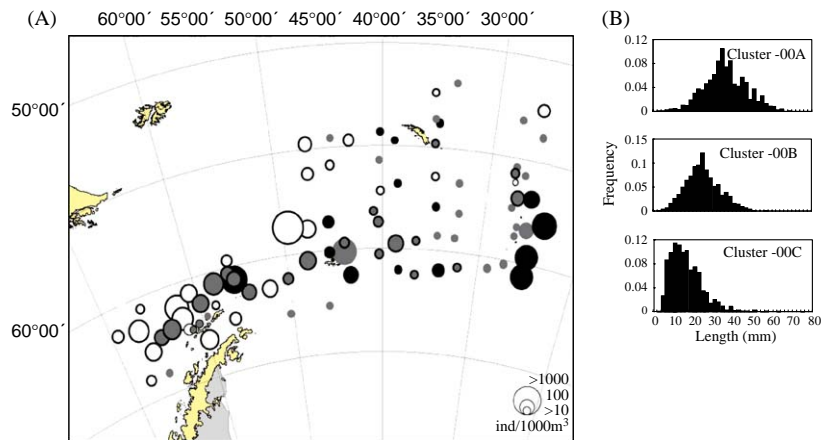


Fig. 5. (A) Spatial distribution and density (ind/1000 m³) of clusters. ○: Cluster 00A. ●: Cluster 00B. ●: Cluster 00C. ●: Cluster analyses not performed. (B) Size distribution (mm).

smaller salps also were observed at a station to the north of Elephant Island.

3.1.2.2. Solitary form. Owing to the low number of solitary forms caught, and because counts were not made on two of the four ships, cluster analysis could not be done. However, length–frequency distributions were compiled for the Antarctic Peninsula and Scotia Sea areas (Fig. 3B).

Size composition in the Antarctic Peninsula area showed two groups (20–60 mm and 80–150 mm). The smaller group mainly comprised animals <50 mm. These were probably immature and so would not have contributed to asexual reproduction through budding of aggregate forms (Foxton, 1966). Conversely, the larger group with a mode at 100–120 mm may have represented older stages that already had released most of their aggregate chains (Foxton, 1966).

In contrast, the size composition in the Scotia Sea covered a wide range (0–120 mm) with a mode at 20–40 mm. Almost half of these solitary salps were <60 mm and so were yet to mature. The remainder were 60–100 mm in length and may have been actively budding aggregate chains.

3.1.3. Clusters and environmental factors

Average temperatures, salinities, and Chl-*a* concentrations in the upper 200 m for Clusters 00A, 00B, and 00C within the area of the Antarctic

Peninsula, the Scotia Sea, and the South Sandwich Islands are shown in Table 2. A consistent pattern of higher average temperatures in clusters with larger size modes was observed in all areas (00A > 00B > 00C). No clear trends were observed for salinity or Chl-*a* concentration. Kolmogorov–Smirnov tests were used to test for significant differences in surface temperature between the clusters in each area (Table 3). In the Scotia Sea, significant differences in temperature distribution occurred between Clusters 00A and 00B, and between Clusters 00A and 00C. No significant differences were observed between Clusters 00B and 00C in the Scotia Sea or between any clusters in the Antarctic Peninsula or South Sandwich Island areas.

One of the reasons for the lack of statistical significance may be the small sample sizes in many of the pair-by-pair comparisons.

3.2. November/December 1994—Elephant Island area

During the first of the two surveys in the Elephant Island area (Kattner and Fütterer, 1995) the highest abundance was 43.2 ind/1000 m³ and the mean 3.8 ind/1000 m³ (Table 1). High abundance was observed to the northwest of the Elephant Island grid (Fig. 6A). Cluster analysis showed three clusters at a similarity level of 0.78

Table 2

Average temperatures, salinities, and surface chlorophyll concentrations in the upper 200 m for the three clusters observed during the CCAMLR 2000 Survey

	Temperature			Salinity			Chlorophyll		
	Mean	S.E.	<i>n</i>	Mean	S.E.	<i>n</i>	Mean	S.E.	<i>n</i>
Antarctic Peninsula									
Cluster 00A	0.94	0.32	12	34.24	0.05	12	0.85	0.24	11
Cluster 00B	0.83	0.16	10	34.50	0.33	10	0.68	0.20	8
Cluster 00C	0.78	n.a.	1	34.38	n.a.	1	3.19	n.a.	1
Scotia Sea									
Cluster 00A	1.47	0.26	9	34.07	0.77	9	1.64	0.35	9
Cluster 00B	0.24	0.29	9	34.41	0.13	9	1.54	0.30	10
Cluster 00C	0.12	0.26	11	34.18	0.05	11	1.37	0.36	11
South Sandwich Islands									
Cluster 00A	2.64	n.a.	1	33.91	n.a.	1	0.20	n.a.	1
Cluster 00B	1.58	0.27	2	34.10	0.07	2	1.12	0.53	2
Cluster 00C	−0.04	0.30	4	34.25	0.09	4	0.43	0.09	22

n.a.: not available

Table 3

Non-parametric tests (Kolmogorov–Smirnov) comparing average temperatures in the upper 200 m for the various cluster combinations within each area

	<i>n</i>	χ^2	<i>p</i>
Antarctic Peninsula			
Clusters 00A and 00B	12, 10	1.024	>0.999
Clusters 00A and 00C	12, 1	1.256	>0.999
Clusters 00B and 00C	10, 1	1.782	0.821
Scotia Sea			
Clusters 00A and 00B	9, 9	10.889	0.009
Clusters 00A and 00C	9, 11	8.018	0.036
Clusters 00B and 00C	9, 11	0.729	>0.999
South Sandwich Islands			
Clusters 00A and 00B	1, 2	2.667	0.527
Clusters 00A and 00C	1, 4	3.200	0.404
Clusters 00B and 00C	2, 4	5.333	0.140

(Fig. 4B): Cluster 94A, a large size group (main size range 8 to 26 mm with a mode at 20 mm); Cluster 94B, a middle size group (main size range 10 to 32 mm, with the main mode at 14 mm and smaller modes at 20 and 30 mm); and Cluster 94C, a small size group (main size range 6 to 28 mm with modes at 8 and 12 mm, and a small additional mode at 26 mm) (Fig. 6B). The area of high abundance was mainly toward the northwest of

the survey grid, where most of the stations belonged to Cluster 94A. Clusters 94B and 94C were fewer in individual numbers compared to Cluster 94A and distributed to the southeast of Cluster 94A. Densities in the southeast half of the grid were extremely low.

3.3. December 1996—Elephant Island area

During the second of the two surveys in the Elephant Island area (Kattener, 1998), *S. thompsoni* was distributed widely and in high abundance, with the exception of the area to the south and northwest of Elephant Island where density was low (Fig. 7A). The highest abundance was 1041.4 ind/1000 m³ and the mean 110.7 ind/1000 m³ (Table 1). The length–frequency distribution was clustered into three groups at a similarity level of 0.8 (Fig. 4C): Cluster 96A, a large size group (main size range 12–50 mm with multiple modes between 24 and 44 mm); Cluster 96B, a middle size group (main size range 6–36 mm, with a main broad peak and a mode at 20 mm); and Cluster 96C, a small size group (main size range 6–34 mm with a mode at 12 mm) (Fig. 7B). Cluster 96A mainly occurred to the north of Cluster 96B. Cluster 96C mainly occurred at the southern edge of Cluster 96B.

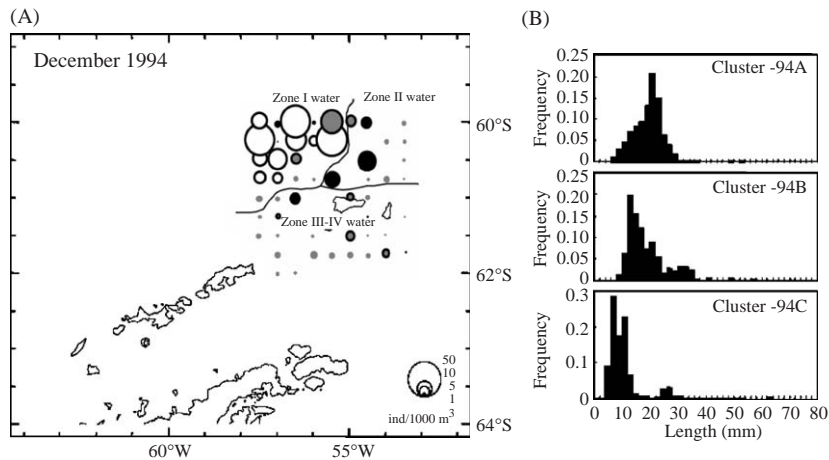


Fig. 6. (A) Density distribution of salps (solitary plus aggregate forms) in the Elephant Island area in November/December 1994. ○: Cluster 94A. ●: Cluster 94B. ●: Cluster 94C. ●: Cluster analyses not performed. Water masses based on a survey in January 1995 (AMLR, 1995). (B) Size distribution (mm).

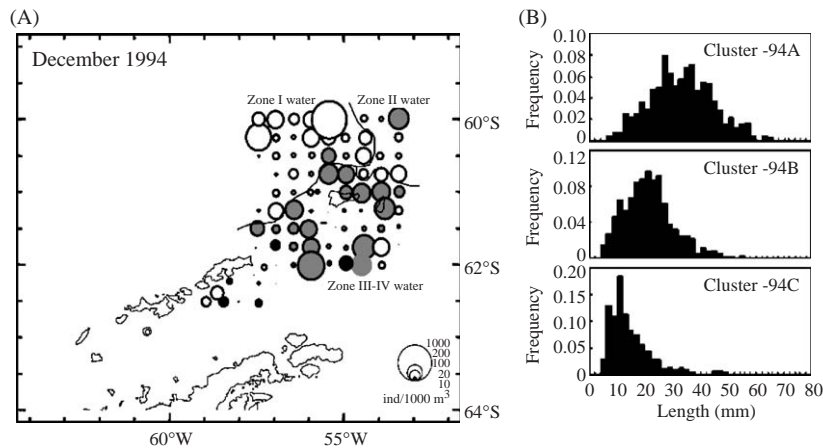


Fig. 7. (A) Density distribution of salps (solitary plus aggregate forms) in the Elephant Island area in December 1996. ○: Cluster 96A. ●: Cluster 96B. ●: Cluster 96C. ●: Cluster analyses not performed. Water masses based on a survey in January 1997 (AMLR, 1997). (B) Size distribution (mm).

3.4. Daily carbon demand

Carbon demand was calculated from the length–frequency distribution and abundance data using a carbon–length relationship (Huntley et al., 1989). Daily carbon demand per m^2 per day was calculated by assuming a daily carbon demand of

25% of body carbon (Huntley et al., 1989) (Fig. 8). For each of the three surveys, the mode occurred in the lowest increment: $0\text{--}5\text{ mg C m}^{-2}\text{ d}^{-1}$. In the Elephant Island area, there was a higher carbon demand in the 1996/97 season than the 1994/95 season. This could be explained by the effect of higher salp abundance plus larger individual size.

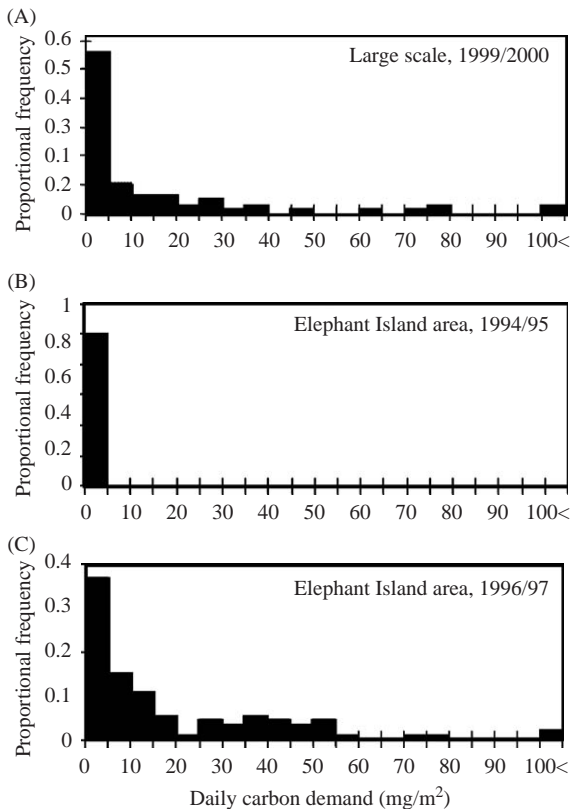


Fig. 8. Frequency distributions of daily carbon demand (mg Cm^{-2}). (A) CCAMLR 2000 Survey. (B) Elephant Island area, November/December 1994. (C) Elephant Island area, December 1996.

4. Discussion and conclusions

4.1. Abundance and distribution

The large-scale distribution of water masses during the CCAMLR 2000 Survey (Brandon et al., 2004) showed the influence of Weddell Sea water at the southern Scotia Sea stations. Krill distributions also indicated outflow from the Weddell Sea krill population into the Scotia Sea, which implies a strong influence of Weddell Sea water during the 1999/2000 season (Siegel et al., 2004). According to Foxton (1966), *S. thompsoni* is an animal of the mid Southern Ocean latitudes ($45\text{--}55^\circ\text{S}$) and is generally absent from the Weddell drift (now termed the Weddell Gyre) and the high-latitude region of the East Wind drift (now termed the

Antarctic Coastal Current). Salp abundance in the 1999/2000 season generally followed the same pattern, however, salp abundance in the central Scotia Sea was also low (Fig. 2).

Salps are filter feeders that collect food particles using mucous nets (Aldredge and Madin, 1982). These mucous nets can become clogged when filtering very high concentrations of particles (Harbison and Gilmer, 1976), which may exclude salps from areas of unusually high particle concentration (Harbison et al., 1986). Chl-*a* concentrations and primary production values (Holm-Hansen et al., 2004) were high in the central Scotia Sea where salp densities were low in the Antarctic Peninsula area and around the South Sandwich Islands where salp abundance was high.

Perissinotto and Pakhomov (1998) found a dramatic reduction in salp feeding rate when the Chl-*a* concentration exceeded a threshold level of $1\text{--}1.5 \mu\text{g Chl-}a \text{ l}^{-1}$, which lead to the collapse of the salp population. This supports the results of the present survey where low numbers of salps occurred when the Chl-*a* concentration was $> 1 \text{ mg m}^{-3}$ (Fig. 9).

The Salpidae are known to repeat alternations of generations between an asexually reproducing

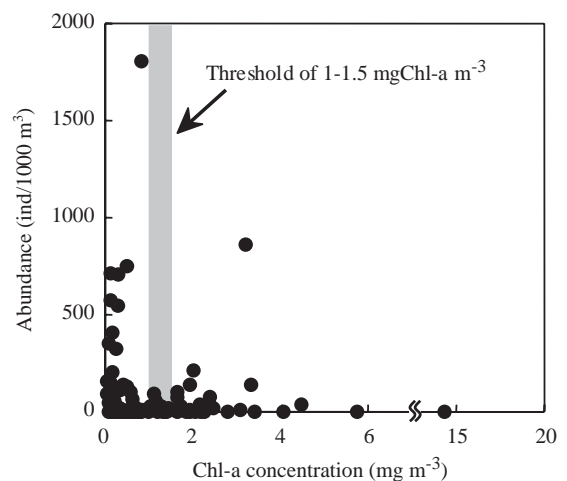


Fig. 9. Scatter plot of salp abundance against surface chlorophyll concentration. Hatched area denotes the threshold chlorophyll concentration reported by Perissinotto and Pakhomov (1998).

generation and a sexually reproducing generation (Nishikawa et al., 1995). Bursts or rapid increases in the salp population are caused by asexual reproduction (budding). Daponte et al. (2001) demonstrated that the formation of swarms is directly dependent on the number of buds per block of each solitary specimen. These studies imply that optimal food conditions may lead to higher numbers of buds, and if linked with the high abundance of a seed population (solitary forms) it will eventually lead to the formation of intense blooms of salps. In the present study, the density of solitary forms in the Scotia Sea was lower than around the Antarctic Peninsula (Table 1). Also, the Chl-*a* concentration in the central Scotia Sea was above the threshold at which the feeding rate dramatically reduced. These factors may have combined to restrict salp abundance to low levels in this area.

There are other possible explanations for this inverse relationship between salp abundance and Chl-*a* concentration. For example, salps may have grazed down the phytoplankton community (Loeb et al., 1997). During the present survey, the daily carbon demand by salps is estimated at $<10 \text{ mg m}^{-2}$ at 57% of stations, and $<20 \text{ mg m}^{-2}$ at 80% of stations (Fig. 8). In contrast, El-Sayed and Weber (1982) estimated daily primary production rates of $100\text{--}1400 \text{ mg C m}^{-2}$ throughout the Scotia Sea. In the Elephant Island area, daily carbon demand at all stations in the 1994/95 season was $<5 \text{ mg m}^{-2}$. In the 1996/97 season, daily carbon demand was $<30 \text{ mg m}^{-2}$ at 74% of stations. These values are less than 10% of the mean productivity of $374 \text{ mg C m}^{-2} \text{ d}^{-1}$ estimated for the Elephant Island area in 1990–1993 (Helbling et al., 1995). Thus, it seems unlikely that grazing pressure would have been high enough to have had a major effect on the levels and distribution of Chl-*a*.

Another possible explanation is biological segregation between salps and krill, forcing salps to concentrate in areas of lower phytoplankton density (Nishikawa et al., 1995). Examination of the krill (Siegel et al., 2004) and salp distributions shows some separation between krill and salps in the northern Scotia Sea, with salps occurring more frequently in the central Scotia Sea and krill occurring more frequently between South Georgia

and the South Sandwich Islands. However, there was also significant overlap in the distribution of krill (Siegel et al., 2004) and areas of high salp abundance, particularly in the southern part of the survey region around the South Shetland Islands, the South Orkney Islands, and the South Sandwich Islands. On the basis of the evidence obtained in this study it is concluded that salp abundance and distribution probably reflect the interaction of salps with their food supply, with salps unable to feed effectively in areas of high Chl-*a* concentration.

4.2. Size composition and distribution

In the Antarctic Peninsula area, there is a marked zonation in salp size with large salps (Cluster 00A) occurring offshore of the South Shetland Islands and in the Bransfield Strait and smaller salps (Cluster 00B) present in a narrow band along the shelf edge to the north of the South Shetland Islands (Fig. 5A). The boundary between these clusters is characterized by a frontal zone containing a shear current with slow currents inshore of the front (Ichii et al., 1998). Such structures may act to retain organisms passively advected onto the shelf and so generate the observed distribution patterns.

Tunicate growth rates are known to be temperature dependent when other factors are constant (King, 1982; Paffenhofer, 1976). Thus, salps living in warmer waters may grow faster than salps found in cooler waters. Certainly, during this study larger salps (Cluster 00A) generally occurred in the northern Scotia Sea while smaller salps (Clusters 00B and 00C) occurred to the south and around the South Sandwich Islands. Stations with salps of larger size tended to occur where temperatures were relatively high and vice versa (Table 2). Increased salp by-catch in krill fisheries at higher temperature conditions (Kawaguchi et al., 1998) also supports the idea that salps grow faster in warmer waters (Table 3). Temperature also affects the timing of the intense budding period; salps in warmer water bud earlier and so have a longer growth period. Foxton (1966) used the size of aggregate salps as an indicator of time since active bud release; thus swarms containing

salps of modal size 5–10 mm (such as in Cluster 00C) represent swarms undergoing active bud release, while larger sizes can be used to indicate time since budding occurred. Given the distribution of these clusters (Fig. 5A), earlier budding may have taken place along the Antarctic Peninsula and the northern edge of the Scotia Sea, where temperatures were relatively high. A similar distribution was observed in the Indian Ocean with latitudinal variation in the composition of developmental stages due to a decrease in budding activity from north to south, and a temporal succession of stages (Casareto and Nemoto, 1986).

The same spatial distribution in salp size was seen in the Elephant Island area in 1994/95 and 1996/97. Although the mean densities were substantially different for the two surveys, on both occasions larger salps occurred to the northwest of the survey grid and smaller salps to the southeast. Huntley et al. (1989) also observed a spatial separation of size groups and concluded that the larger size groups were advected from upstream areas along the Antarctic Peninsula where smaller salps were found. Siegel and Harm (1996) also observed regional differences in salp abundance and size in the southern Bellingshausen Sea. Larger salps were found in high abundance to the north under the influence of the Antarctic Circumpolar Current, while smaller salps in low numbers occurred in the southern waters of the Antarctic Coastal Current. The authors concluded that salps on the southern shelf were advected in from the oceanic region and trapped in unfavorable conditions where dense ice cover and low phytoplankton concentrations inhibited salp growth and recruitment.

Amos (2001) observed a general temperature gradient in the surface waters around Elephant Island, with high temperatures to the northwest decreasing toward the southeast, and with the boundaries of five water zones running in a southwest to northeast direction across the survey grid (Helbling et al., 1995). In the present study, the different size groups do not appear to fit with the upstream/downstream relationship proposed by Huntley et al. (1989), but with water masses (Figs. 6 and 7). The larger clusters were confined to Zones I and II; waters of the warm Antarctic

Circumpolar Current. It seems likely therefore, that at a range of spatial scales variation in the size structure of the salp population could be explained by variations in water temperature.

4.3. A spatio-temporal pattern of salp budding (asexual reproduction)

Given the ability of salps to reproduce rapidly under favorable conditions, and their characteristically patchy distributions (Alldredge and Madin, 1982), regular sampling could be expected to result in an unstructured distribution of size groups. However, there appears to be a synchronous pattern in size composition relative to the isotherms presented by Brandon et al. (2004); with larger size groups found in warmer waters (Tables 2 and 3). This implies that the period of intense budding and the growth rate were generally synchronized within waters of similar temperature, and that budding was earlier in the warmer waters. This idea is also supported by the two smaller scale surveys in the Elephant Island area. In both, size composition was defined by the water masses (Figs. 6 and 7), and there was also an indication of earlier budding in warmer waters. Furthermore, the 1996/97 season, which had higher water temperatures than the 1994/95 season (Amos, 2001), had greater salp abundance and larger sizes.

Throughout this investigation, there has been a clear indication that water temperature is the principal factor governing the timing of intense budding, although it was also evident that salp feeding is inhibited above a certain level of phytoplankton concentration. Since water temperature decreases from north to south, and increases as the season progresses from spring to summer, the general spatio-temporal pattern of salp budding events may be taken as proceeding from north to south. Ice-edge phytoplankton blooms proceed south as the ice edge retreats (Lancelot et al., 1993). Such blooms mainly comprise large chain-forming diatoms (Socal et al., 1997), which may be grazed down by the high grazing pressure of krill swarms passing through the area in summer (Tréguer et al., 1991). Thus, it could be speculated that areas of intense salp budding progress southward through the season,

following the phytoplankton bloom, but with a delay between the phytoplankton bloom and the increase in salp numbers during which krill graze the dense phytoplankton bloom to a level at which salps can feed effectively.

This study concerns single surveys for each season. To corroborate the spatio-temporal succession proposed here further details are required on the maturity status of rapidly growing salps. Further analyses of preserved samples from the CCAMLR 2000 Survey would be useful for a better understanding of salp ecology.

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